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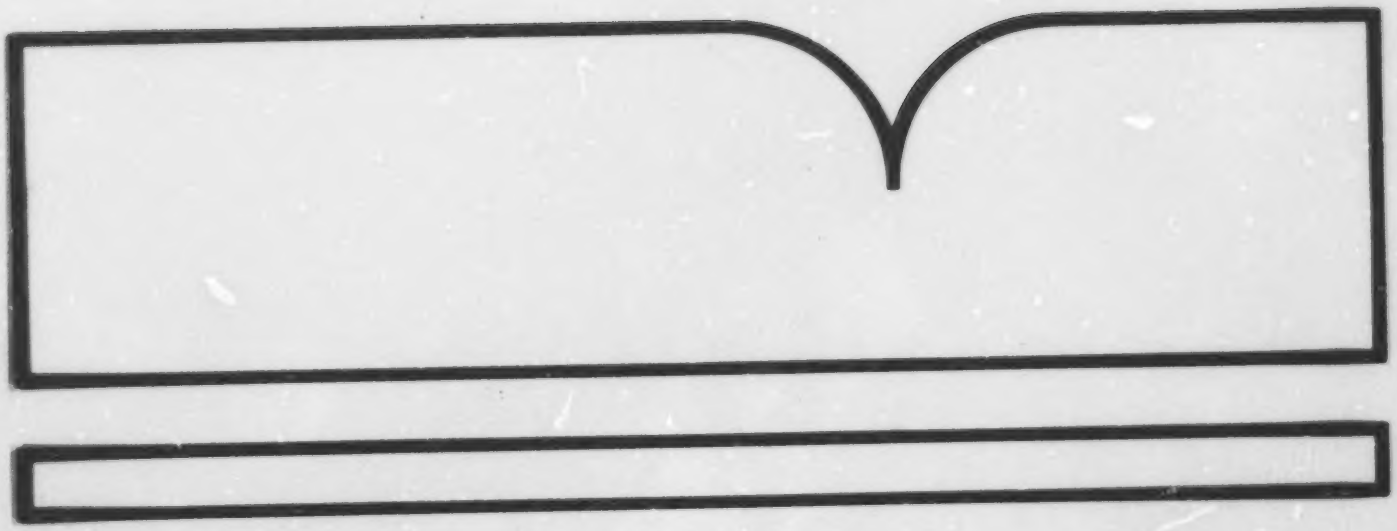

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16. ABSTRACT

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Demographic evaluation of the influence of temperature and salinity on the copepod *Eurytemora herdmani*

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ABSTRACT: Demographic responses of the estuarine copepod *Eurytemora herdmani* to several combinations of temperature and salinity were evaluated in the laboratory. Observed values of the intrinsic rate of population increase, *r*, ranged from $-0.069\ d^{-1}$ to $0.088\ d^{-1}$. Over the experimental range of 15 to 35 ‰ and 10 to 20 °C, the observed values of *r* at 20 to 30 ‰ were higher than those at 15 or 35 ‰; observed values of *r* at 20 °C were lower than those observed at the lower temperatures. Temperature was found to influence the rate of population growth primarily through age of reproduction while salinity effects were primarily through fecundity. The extrapolated limits of temperature and salinity permitting population growth were generally consistent with reported occurrences of *E. herdmani* in the field.

INTRODUCTION

It was largely through the writing of G. E. Hutchinson that the concept of niche received the dimensional formulation on which much later work was based. In his classic article of niche theory, Hutchinson (1958) suggested that niches can be characterized by population responses to ecological variables. For each of the ecological factors relevant to a species there exist limiting values between which individuals of the species can reproduce and survive indefinitely. Together, these limiting values of each of the pertinent factors delineate the boundaries of a multi-dimensional hypervolume, in which every point corresponds to a state of the biological and physical environment, permitting the survival and reproduction of the species. Hutchinson's formulation of the hypervolume niche was anticipated by the work of Birch (1953), who had already used *r*, the intrinsic rate of population increase, to examine the distribution of 3 species of grain beetles. Laboratory cultures of the beetle species were exposed to several combinations of temperature and moisture content of the grain, demonstrating that 2 critical dimensions may be very useful in examining a species' potential and realized distributions.

I examined the population response of the marine copepod *Eurytemora herdmani* Thompson and Scott, 1897, to 2 environmental variables known to be important to the distribution of the species. Salinity and temperature have been shown by others (e.g. Jeffries, 1962) to be important regulators of estuarine copepod distributions. Salinity and temperature offer another advantage as environmental dimensions of interest: they are often included in published records of species' distributions, allowing comparison with laboratory results. Partial bounds for this copepod and a related species, *Eurytemora affinis*, have been reported by Katona (1970). Using ability to reproduce successfully as his criterion, Katona found limiting values of salinity to be 16 and 33 ‰ and limiting values of temperature to be 2 and 19 °C.

The straightforward criterion of successful reproduction does not, however, describe a graded measure within the limiting values. The primary measure of population response used here was *r*, the intrinsic rate

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of population increase. This statistic was chosen because it expresses in a single value the combined effect of survivorship, fecundity, and age of reproduction on population growth. Rate of population increase is not a universally applicable measure of habitat quality but it is appropriate for estuarine copepods because their environment is patchy (Raymont, 1980), demanding rapid population response when conditions become favorable. Ability to reproduce quickly would seem to be a good indicator of population well-being. Other measures of habitat quality used were age of reproduction of the youngest female in a cohort to reproduce and age at death of the longest-lived female in a cohort, both indicators of development rate; mean brood size and mean number of broods produced by a breeding female in her lifetime, both indicators of fecundity; and frequency of survival to the age of sexual maturity.

Mapping the population response of *Eurytemora herdmani* in the laboratory reveals important characteristics about the species' population tolerances and responses within its critical environmental limits. Although laboratory-derived values of environmental tolerances must be applied with care to field situations, general patterns of response can be quite revealing. Comparison of its potential with its actual field distribution will contribute to studies of its interactions with the closely-related species *Eurytemora americana* and *E. affinis* and other copepods, zooplankton, and phytoplankton.

METHODS

Culture techniques. Water for culture was collected at high tide from the Pettaquamscutt River approximately 2 miles upriver from its mouth on Narragansett Bay. Salinities at the collection times were 28 to 30 ‰. The water was stored in 20 l Nalgene carboys at 2 °C, then passed through a Gelman 0.45 µm pore membrane filter before use. Test media of different salinities were prepared from a concentrated stock made by heating the filtered water to 40 °C for 48 h to raise the salinity to 50 ‰, by evaporation. Concentrated stock was mixed 1:1 with Pettaquamscutt River water of 28 to 30 ‰ and then diluted with deionized water to the desired salinity.

Copepods used in this research were obtained from a continuous culture maintained at the US EPA Environmental Research Laboratory at Narragansett, Rhode Island. The stock culture is maintained at a temperature of 15 °C and a salinity of 28 to 30 ‰, conditions very close to those prevailing when the copepods were collected. Copepods had been in culture about 4 mo at the start of this experiment. For this study, the copepods were maintained in static culture in 75 ml Carolina dishes at densities of 1 individual 3 ml^{-1} for nauplii and 1 indiv. 5 ml^{-1} for copepodids. Loosely-capped scintillation vials of 22 ml capacity were found satisfactory for isolating mating pairs of adults. Temperatures were maintained within ±1 C°. The light cycle used was L:D 12:12. The copepods were fed *Skeletonema costatum, Monochrysis lutheri, Tetraselmis suecia*, and *Rhodomonas baltica* at an average total concentration in the medium of 40,000 cells ml^{-1} as determined by hemacytometer count. This concentration is above that found saturating for the related copepod *Pseudocalanus* (Corkett and McLaren, 1970). The algae were raised statically in F/2 medium (Guillard and Ryther, 1962) at 25 ‰ salinity. The copepods were fed at intervals of 1 to 2 d and culture water was changed every 4 to 5 d, minimizing the possibility that deterioration of the algal food under unsuitable temperature and salinity conditions might appreciably influence experimental results.

Experimental protocol. Breeding adults were removed from the stock culture and gradually acclimated to the desired temperature and salinity. Temperature was changed by no more than 5 C° in 48 h and salinity by no more than 3 ‰. Only nauplii obtained from the adults after acclimation were used for the test. Cohorts of 100 to 200 nauplii hatched within 24 h were brought to maturity at temperatures of 10, 15, 17.5 and 20 °C at salinities of 15, 20, 25, 30 and 35 ‰. At sexual maturity, individual females were isolated with a single male raised under the same conditions and checked daily for the remainder of their lives. Nauplii produced were removed and counted. Dead males were replaced promptly. Survivorship and fecundity of all females reared at a given temperature and salinity were pooled to calculate a life table for that set of conditions.

The values of r were calculated using the equation developed by Lotka (1925):

$$1 = \sum_{x} e^{-rx} l_x m_x \qquad (1)$$

where l_x = probability of surviving to age x; m_x = the expected fecundity at age x. This equation must be solved by iterative techniques. It can be applied only to populations where the l_x and m_x functions are constant, conditions leading to exponential growth that are seldom met in nature but can be reasonably applied in the laboratory if stocks are adequately housed and food is suitable and abundant.

Data on development time, longevity, brood size, brood number and r were compared among treatments by analysis of variance techniques. Data on survivorship, sex ratio, and r were related to salinity and temperature by multiple linear regression and non-

linear regression. Angular transformation was applied to survival frequencies and sex ratios before regression analysis (Snedecor and Cochran, 1980). Duncan multiple range tests were also performed on development time, longevity, survivorship, brood size, brood number, and r data. A single population binomial hypothesis test was used to determine significant skewing of the sex ratio.

RESULTS

Both development time and longevity of the experimental populations of *Eurytemora herdmani* were significantly dependent upon temperature ($p < .0001$). Individuals raised at lower temperatures matured more slowly but lived longer (Fig. 1). Salinity had no significant effect on longevity ($p = .92$) or maturation time ($p = .88$).

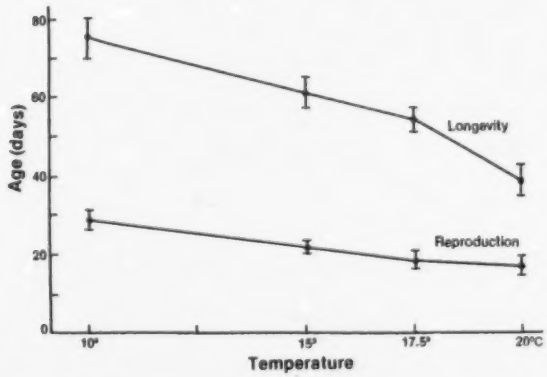

Fig. 1. *Eurytemora herdmani*. Effect of temperature on maximum longevity and first day of reproduction of females reared in all salinities. Upper line: mean age at death of longest-lived female; lower line: earliest day of reproduction at each experimental condition. Salinity had no significant effect on these phenomena. Error bars: ± 1SD of values from all salinities

Survival to the age of first reproduction of females reared at 25 ‰ was statistically dependent on temperature ($n = 301$) ($p < .05$), but there was no significant relation between temperature and survivorship to maturity among females reared at other salinities ($n = 1094$).

The sex of the developing copepods could not be determined until they approached maturity. The sex ratio observed at sexual maturity was skewed toward males, differing significantly from 1:1 ($p < .05$). There is an indication of a linear relation between the extent of mortality of the undifferentiated immatures and the observed sex ratio at maturity ($p = .06$), with high premature mortality reducing the proportion of females

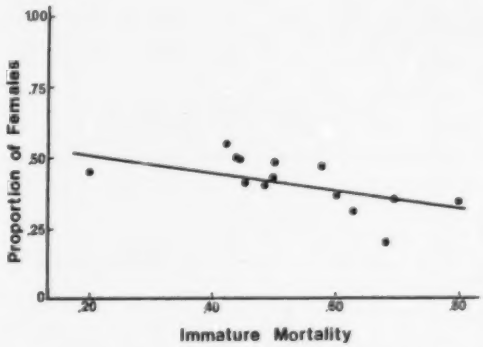

Fig. 2. *Eurytemora herdmani*. Effect of mortality of undifferentiated immature individuals (male and female) on the sex ratio observed at sexual maturity (proportion of females). Each point represents the observed immature mortality and subsequently determined sex ratio at one temperature and salinity combination

(Fig. 2). Sex ratios determined at maturity from only the 50 % of the cohorts with the lowest premature mortality were not significantly different from 1:1 ($p < .05$). Based on this result, supported by observations of McLaren (1976), who also found a near-1:1 sex ratio in *Eurytemora herdmani*, sex ratios at birth were assumed to be 1:1 for all subsequent population calculations.

The number of broods produced by each female was dependent on salinity ($p < .0001$) and temperature ($p < .0001$). Females reared at salinities of 20 to 30 ‰ produced significantly more broods ($p < .05$) and larger broods ($p < .05$) than females reared at 15 or 35 ‰ (Fig. 3 and 4). Females reared at 20 °C produced fewer broods ($p < .05$) and smaller broods ($p < .05$) than females reared at lower temperatures (Fig. 3 and 4).

The value of r was influenced significantly by salinity ($p = .05$) and temperature ($p = .008$). The lowest values of the intrinsic rate of population increase occurred at the highest temperature ($p < .05$). An acceptable overall fit ($r^2 = .81$) of these data is achieved with a model that incorporates both linear effects of temperature and salinitiy, and second-order effects. This model suggests a biological optimum may exist at the intermediate values of the variables (Table 1). A contour plot of the model in Table 1 takes the shape of a dome (Fig. 5).

DISCUSSION

The most influential statistic on the value of r is the age at reproduction, which enters into the Lotka (1925) equation as an exponential. Because the initial days of reproduction are weighted most heavily, r is very sensitive to changes in age at first reproduction (Cole, 1954). In *Eurytemora herdmani*, the age at first reproduction was observed to be strongly influenced by

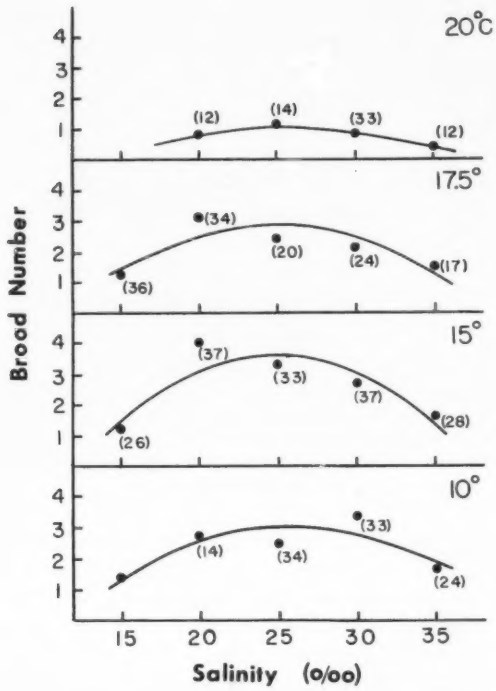

Fig. 3. *Eurytemora herdmani*. Effect of temperature and salinity on mean number of broods produced by each mature female. Total numbers of mature females used are indicated in parentheses

temperature but not to a significant degree by salinity. Individuals reared at low temperatures experienced delayed maturation (Fig. 1). Katona (1970) also found that generation times (defined as the time from egg to reproductive female) of *E. herdmani* populations raised at low temperature were longer than those of populations raised at higher temperatures. Others (e.g. Deevey, 1960; McLaren, 1965, 1974, 1976; Heinle, 1969; Geiling and Campbell, 1972; Landry, 1975) have noted a general decrease in copepod development rate at lower temperatures. Since a late age of first reproduction tends to reduce the rate of population growth (other factors held constant), the general effect of reduced temperature is to reduce the value of *r*.

The other population statistics that influence the rate of population growth are l_x, the probability of survival to age x, and m_x, the fecundity during the interval x to x+1. The magnitude of the total survivorship contribution to the value of *r* is most strongly influenced by the frequency of survival to the age of first reproduction, since the exponential effect of the age factor causes the initial days of reproduction to be weighted most heavily on calculating *r*. There is an indication that an effect of reduced temperature was to promote the survival of immatures to the age of sexual maturity, thus tending to decrease *r*.

The overall effect of salinity tended to reduce the value of *r* at the highest and lowest salinities through its effect on fecundity. Fecundity in copepods is determined by the number of offspring in a brood and the number of broods a female can produce in her lifetime. Both brood size and brood number were observed to decline at the highest and lowest salinities tested.

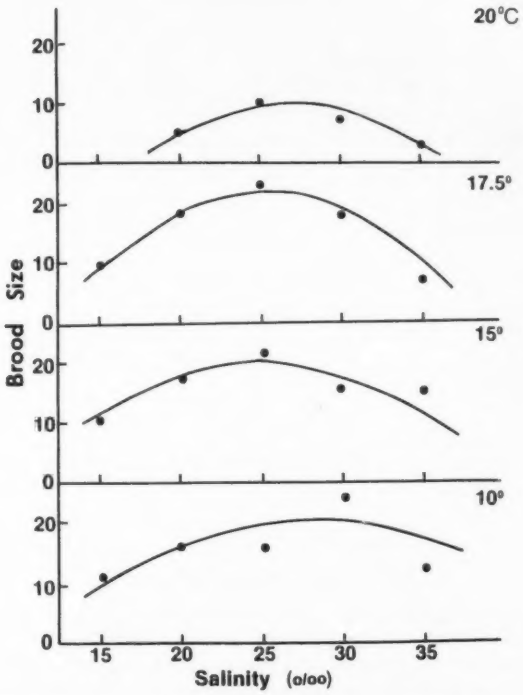

Fig. 4. *Eurytemora herdmani*. Effect of temperature and salinity on mean total brood size (male and female offspring). Lines represent fitted curves

Table 1. Regression analysis of *r*

Source	Degrees freedom	Sum squares	F-ratio	P
Model	5	0.02044	11.24	.0002
Salinity	1	0.00059	1.62	.226
Temperature	1	0.00453	12.47	.004
Salinity^2	1	0.00605	16.64	.001
Temperature^2	1	0.00828	22.77	.0004
Salinity × temperature	1	0.00098	2.70	.124
Error	13	0.00473		
Total	18	0.02516		

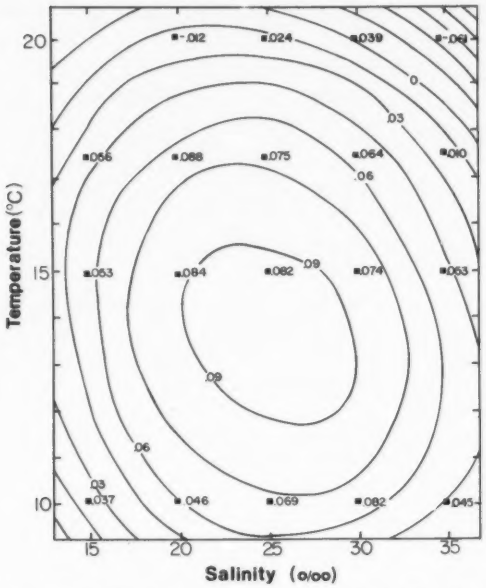

Fig. 5. *Eurytemora herdmani*. Contour plot of effect of temperature and salinity on intrinsic rate of population increase, r; computer generated best-fit model (Table 1). Surface is described by the equation:

$$r = -.609 + -.059\ T - .002\ T^2 + .024\ S - .0004\ S^2 - .0003\ ST$$

where r = intrinsic rate of population increase (d^{-1}); T = temperature (°); S = salinity (‰)

Reduction of fecundity at environmental extremes is also suggested by the work of Katona (1970), who found that *Eurytemora herdmani* individuals could survive and reach maturity at high and low salinities but could not reproduce. *E. affinis* can survive for extended periods of salinities up to 35 ‰, but in the field reproductive populations were not found above salinities of 22.5 ‰ (von Vaupel-Klein and Webber, 1975). Copepods that are reproducing may be unable to cope with extreme changes in salinity. Lance (1964) found that non-reproductive adults of *Acartia* spp. and *Centropages* spp. are appreciably more tolerant to elevated salinity than reproductive adults.

The effect of temperature on brood size and number has received more attention by other workers. Fecundities of several copepods have been predictably linked to temperature (Corkett and McLaren, 1969, 1970). High temperatures have been generally correlated with smaller brood size (Allan and Goulden, 1980). There is an underlying relation between temperature, body size, and brood size, in that copepods reared at lower temperatures have been observed to mature at larger size (Deevey, 1960; McLaren, 1963; Heinle 1969; Rippingale and Hodgkin, 1974); and larger individuals produce larger broods (Ravera and Tonolli, 1956; McLaren, 1965). Katona (1970) and McLaren (1976) found that body size, and by implication, brood size, in *Eurytemora herdmani*, however, is not always predictable from temperature conditions during rearing. My data agree, as over the experimental range brood size was not influenced by temperatures except at the highest temperature tested. Brood number was also not predictable from temperature.

The observed values of r are in general agreement with those found by Lonsdale (1981) for the copepod species *Scottolana canadensis* (.01 to 19 d^{-1}) and *Oithona colcarva* (.05 to 15 d^{-1}). They are lower than those reported for *Eurytemora affinis* at 18 °C (.18 d^{-1}) (Daniels and Allan, 1981).

Temperature and salinity exert different and sometimes opposing effects on the separate population parameters that influence the value of r. Temperature would appear to influence the rate of population growth primarily through its effects on the age of reproduction, while salinity influences rate of population growth primarily through its effects on fecundity. The interaction of temperature and salinity effects is responsible for the variation in population growth rates observed in this study.

Eurytemora herdmani is reported to occur from Narragansett Bay north to Labrador (Carter, 1965), Dolphin and Union Strait on the Bering Sea coast (Johnson, 1958, 1966), Chukchi Sea, Beaufort Sea, Okhostsk Sea, and the Sea of Japan (Heron, 1964). Reported temperatures and salinities are summarized in Table 2.

Population growth rates observed in the laboratory are generally consistent with reports of occurrences in the field (Fig. 6). Several field reports indicate that *Eurytemora herdmani* individuals have occasionally been found at temperature and salinity conditions permitting survival and even reproduction (Katona, 1970), but outside the range permitting active population growth found in this study (Fig. 6). This is not surprising, since environments fluctuate constantly and even self-sustaining populations may undergo periodic, perhaps seasonal, episodes of decline. The highest rate of population growth I observed for the species occurred at a fairly low salinity and high temperature, where no field occurrences have been reported. While this may reflect the paucity of field reports, *E. herdmani* may also be absent from environments with low salinity and high temperature due to competition by other better adapted species. Possible competitors with *E. herdmani* are *E. americana* and *E. affinis*, whose distributions overlap that of *E. herdmani* (Jeffries, 1967). Katona (1970) showed that *E. herdmani* developed significantly faster than *E. affinis* at 2 °C but lagged behind its congener at temperatures above 15 °C. Relative abundances of *E. affinis* and *E. americana* have been observed to fluctuate predictably in Raritan Bay, corresponding to seasonal temperature and salinity

Table 2. *Eurytemora herdmani*. Reported field occurrences. Seasonal occurrence, temperature and salinity range when species reported present, and conditions observed during population peaks

Location	Reported occurrence	Temperature (°C)	Salinity (‰)	Reference
Narragansett Bay				Martin (1965)
Upper bay	Apr–Aug	6–21	28.5–29.5	
	*Jun	17	29	
Lower bay	Jun–Aug	14–18	31	
	*Jun	14	31	
Cape Cod Canal	Year-round	2.5–20	29–31.5	Anraku (1964)
	*Apr	5	30	
Piscataqua R, NH				Phillips (1976)
Whaleback Reef	Apr–Oct	3–18	27–31	
	*Jun	10	28	
Navy Yard	Feb–Oct	3–19	22–30	
	*Jun	11	26	
Great Bay	Feb–Oct	2–21	17–30	
Marina	*May	15	22	
Damariscotta R, Maine	Year-round	0–20	24–32	Lee (1974)
Beaufort Sea Chuckchi Sea	+Aug	0.02–6.05	25.6–30.1	Johnson (1956) and Ocean. Obser. Pacif. (1960)

* Peak population numbers
+ Single series of samples taken August, 1950

changes (Jeffries, 1967). It is unlikely that predation is a major cause of these fluctuations because decline of one species is accompanied by replacement with a very similar congeneric species.

It is also possible that the performance of this particular culture may not be typical of the species. The culture was started with animals collected in June from Narragansett Bay, near the southern limit of the species' distribution, and maintained under conditions very close to those observed at the time of collection. Bradley (1978) found that *Eurytemora affinis* populations can adapt to temperature changes quite rapidly, while Katona (1970) reported small differences in response to temperature and salinity between strains of *E. affinis* collected near Woods Hole, Massachusetts (USA), and from the Hamble River at Southampton (England). *E. herdmani* individuals collected from a more northerly location might have different optimal temperature and salinity conditions for population growth.

Rate of population increase of *Eurytemora herdmani* is dependent on both temperature and salinity. Temperature appears to influence population growth rate primarily through development rate, while the influence of salinity is primarily exerted on fecundity. Since reported occurrences of *E. herdmani* are generally consistent with the observed population growth rates, laboratory measures of the rate of population increase would seem to be useful predictors of copepod species' potential occurrence in the field and may also serve as

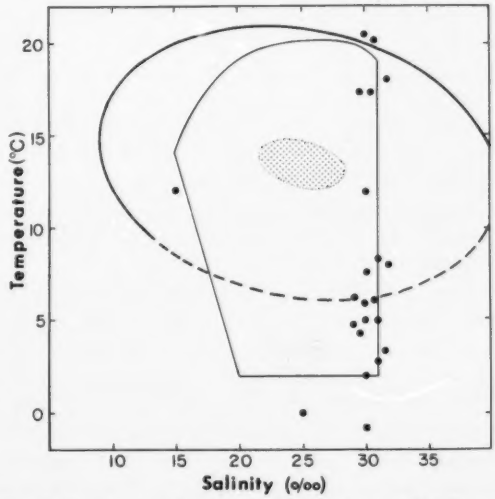

Fig. 6. *Eurytemora herdmani*. Comparison of field reports to laboratory data. Dots: reported *E. herdmani* occurrences in the field; bold line: computer-extrapolation to $r = 0$ of the model in Table 1; solid line: limits of successful reproduction found by Katona (1970); stippled area: region of highest population growth in this study

indicators of possible distributional restrictions caused by other zooplankton species.

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